

**Universitat de Lleida**

Document downloaded from:

<http://hdl.handle.net/10459.1/65092>

The final publication is available at:

<https://doi.org/10.1111/j.1654-1103.2011.01316.x>

Copyright

(c) International Association for Vegetation Science, 2011

# Tree dynamics and coexistence in the montane-subalpine ecotone: the role of different light-induced strategies

**Aitor Ameztegui & Lluís Coll**

**Ameztegui, A.** (Corresponding author, [aitor.ameztegui@ctfc.es](mailto:aitor.ameztegui@ctfc.es)) & **Coll, L.** ([lluis.coll@ctfc.es](mailto:lluis.coll@ctfc.es)):  
*Centre Tecnològic Forestal de Catalunya (CTFC)*, Ctra. Sant Llorenç de Morunys, km. 2; E-25280 Solsona, Spain

**Questions:** Is light availability the main factor driving forest dynamics in the Pyrenean subalpine forests? Do pines and firs differ in their growth, mortality and morphological response to low light availability? Can differences in shade tolerance affect the predictions of future biome changes in the Pyrenean subalpine forests in the absence of thermal limitation?

**Location:** Montane-subalpine ecotones of the Eastern Pyrenees (NE Spain)

**Methods:** We evaluated the morphological plasticity, survival and growth response of saplings of Scots pine, mountain pine and silver fir to light availability in a mixed-forest ecotone. For each species, we selected 100 living and 50 dead saplings and measured their size, crown morphology and light availability. A wood disk at root collar was then removed for every sapling, and models relating growth and mortality to light were obtained.

**Results:** Fir showed the lowest mortality rate ( $< 0.1$ ) at any given light condition. Pines showed comparable responses to light availability although in deep shade Scots pine faced a higher risk of mortality (0.35) than mountain pine (0.19). Pines and fir developed opposing strategies to face light deprivation: fir employed a conservative strategy based on sacrificing height growth, whereas pines enhanced height growth to escape from shade, but at the expense of higher mortality risk. Scots pine showed higher plasticity than mountain pine on all architectural and morphological traits analyzed, showing a higher adaptive capacity to a changing environment.

**Conclusions:** Our results support the prediction of future biome changes in the Pyrenean subalpine forests as silver fir and Scots pine may find appropriate conditions for colonizing mountain pine dominated stands due to land-use change-related forest densification and climate warming-related temperature increases, respectively.

**Keywords:** shade tolerance; montane-subalpine ecotone; morphological plasticity; forest dynamics; *Pinus uncinata*; *Pinus sylvestris*; *Abies alba*; Pyrenees.

**Running head:** Forest dynamics in the montane-subalpine ecotone

## Introduction

Mountain pine (*Pinus uncinata* Ram.) is the dominant species in the subalpine belt of the Pyrenees, whereas Scots pine (*Pinus sylvestris* L.) and silver fir (*Abies alba* Mill.) dominate the montane belt. However, these three species coexist in the ecotone between the upper-montane and lower-subalpine belts, constituting a conifer-mixed forest (Mason et al. 2000, Aunós et al. 2007). The rise in temperatures associated to climate change has prompted predictions of species displacement in mountain areas (Walther et al. 2002, Resco et al. 2006), meaning an upward encroachment of montane species (silver fir and Scots pine) into the subalpine belt can be expected (Walther et al. 2002, Peñuelas et al. 2003, Resco et al. 2006, Peñuelas et al. 2007). Upward spread of species into existing forests is driven not only by climate, but also by interspecific competition for resources and dispersal and establishment patterns (Woodward et al. 1987, Vetaas 2002), as species-specific adaptive responses to the environment and homeostatic effects may modulate changes in community composition (Neilson 1993, Walther et al. 2002, Valladares et al. 2006). Together with increasing temperatures, mountain forests in Spain have also experienced a drastic reduction in logging in recent decades thanks to environmental concerns and the drop in timber profitability. In the absence of large-scale disturbances, this has promoted severe canopy closure and establishment of advanced regeneration of shade-tolerant species such as silver fir (Robakowski et al. 2004, Aunós et al. 2007). In this context, and in the absence of water deficit, interspecific differences in performance under contrasting light conditions can sharply affect the dynamics of these transition areas (Neilson 1993, Delagrange et al. 2004). Light is a highly temporally- and spatially-heterogeneous resource in the forest (Canham 1988, Gravel et al. 2010), and species have developed different abilities to adjust their morphology and physiology to different sets of light conditions (Messier et al. 1999, Delagrange et al. 2004). The way in which species allocate their resources will determine their ability to perform in sun conditions and shade conditions, the latter ability being traditionally dubbed ‘shade tolerance’ (Canham 1988, Valladares et al. 2008). Early classifications of shade tolerance were constructed as relative rankings among species or discrete classes (Baker 1949, Anderson et al. 1969, Whitmore

1989, Ellenberg 1992). The first attempts at quantification related shade tolerance to the ability to maximize carbon gain and growth in shady environments (Bazzaz 1979, Givnish 1988), but more recent studies have reported a trade-off between survival and radial growth at low light (Kobe et al. 1995, Lin et al. 2002, Kunstler et al. 2005). Thus, shade tolerance has been quantified by estimating the relationship between growth and probability of mortality (Kobe 1996, Wyckoff et al. 2000, Wyckoff et al. 2002), producing quantitative estimates of shade tolerance that generally match the previously accepted ranks (Kneeshaw et al. 2006). Accordingly, in low-light ambiances, shade-tolerant species do not necessarily grow faster than shade-intolerants (Canham 1989, Pacala et al. 1994), but will be more likely to survive (Kobe et al. 1997, Canham et al. 1999). Furthermore, shade tolerance has also been suggested to be related to the ability to reduce height growth to avoid the increased respiration and maintenance costs associated with larger size (Messier et al. 1999, Kneeshaw et al. 2006). Overall, the ability to grow and survive in the understory can be achieved by alternative combinations of physiological, morphological, allocational and architectural traits that can be species- and/or environment-specific (Claveau et al. 2002, Delagrange et al. 2004, Valladares et al. 2008) and that are in turn affected by ontogenetic effects, i.e. by the plant size (Niinemets 2006, Sánchez-Gómez et al. 2006b, Lusk et al. 2008).

This study aimed to advance in understanding the different light-induced strategies developed by three conifers (silver fir, mountain pine and Scots pine) in order to coexist in the montane-subalpine ecotones of the Catalan Pyrenees (NE Spain). In today's changing context, potential structure and composition changes are of major concern in these forests, as they constitute the southern distribution limit of endangered plant and animal species, such as the Western capercaillie (*Tetrao urogallus*) or Tengmalm's Owl (*Aegolius funereus*) that are particularly sensitive to changes in their habitat (Camprodon 2001, Gracia et al. 2007). We hypothesize that in the absence of thermal limitation, silver fir and Scots pine would develop more efficient strategies than mountain pine to respond to light variations, which if true would lead to an upward displacement of the montane-subalpine transition zone.

## Methods

### Study area and species

The study area is located on the Pallerols Valley in the Alt Pirineu Natural Park, Catalonia, NE Spain (42°23' N; 1°15' E). Mean annual rainfall at the study site is slightly below 1000 mm, distributed equally among seasons. Mean annual temperature is 6.1°C and, in general, summers are relatively cool (mean temperature around 15°C), meaning there is no summer drought. Winters are long and cold, with a growing period of 173 days and only 150 frost-free days. Forests in the montane belt are occupied by Scots pine (*Pinus sylvestris* L.), a shade-intolerant species that find its optimum at about 1500 m, and by silver fir (*Abies alba* Mill.), one of the most shade-tolerant conifers in the Pyrenees, which grows in the more humid areas between 1200 and 1900 m. Mountain pine (*Pinus uncinata* Ram.), also traditionally considered as a shade-intolerant species, dominates the subalpine belt (1700-2400 m), with its optimum performance at about 1800 m (Blanco et al. 2005, Ruiz de la Torre 2006). Our study site was located between 1700 and 1850 m, in the montane-subalpine ecotone where these three conifer species (silver fir, Scots pine and mountain pine) co-exist. No logging, silvicultural treatments or major disturbances affecting canopy have occurred in the last decade in the study area. The plots were all located on uneven-aged stands characterized by a high horizontal and vertical heterogeneity, therefore presenting gaps alternating with heavily-shaded areas.

### Data collection

Samples were taken along six transects crossing the montane-subalpine ecotone. All transects were located in mixed-conifer stands, with different slopes and aspects. A total of 94 silver fir, 98 Scots pine and 96 mountain pine saplings were sampled, with a sapling defined as a tree above 50 cm in height but below 7.5 cm in diameter at breast height (Camarero et al. 2000). For each sapling, we measured diameter at 10 cm, total sapling height, crown height and crown diameter. Apical growth was determined as the mean value of the length of the last three shoots of the main axis. We also measured lateral growth as the mean length growth of the last three years for at least four branches

per tree, two in the upper third of the sapling and two in the lower one. A wood disk from the root collar of every sapling was removed, dried, sanded and scanned, and annual radial growth was determined as the mean for the last three years according to the method described at Lussier et al. (2004).

Light measurements were taken during September and October 2009, under completely overcast conditions, as proposed by Messier and Puttonen (1995) and Parent and Messier (1996). The percentage of above-canopy light (photosynthetic photon flux density; PPFD) at the top of each sapling was used to describe its light environment. Above-canopy PPFD was measured with a Li-190SA Quantum sensor (Li-COR, Nebraska, USA) placed on an open area adjacent to the study site and connected to a data-logger that recorded readings every 10 seconds. A second quantum sensor was used to measure PPFD at the top of each sapling, and time of the measurement was recorded. Light availability for each sapling was then determined as %PPFD.

## **Growth and mortality as a function of light**

To obtain the relationship of growth and mortality with light, we employed the two-step approach originally developed by Kobe et al. (1995) for the SORTIE model. Thus, we first modeled the relationships between growth and light availability and between mortality risk and past growth, and then combined them to determine the relationship between mortality and light. Radial and apical growth were modeled against light availability (Figure 1). The relationship between growth and light availability was established by a Michaelis-Menten function, which is widely used for modeling tree growth (Pacala et al. 1994, Wright et al. 1998, Lin et al. 2002, Kunstler et al. 2005). According to this function, growth can be expressed as:

$$\text{Equation 1} \quad G = size^d \frac{a * L}{a/s + L}$$

where  $G$  is the growth of an individual of a given size at a light level  $L$  (%PPFD), while  $a$  and  $s$  are the parameters of the Michaelis-Menten function, which can be interpreted as asymptotic growth rate and slope at zero light, respectively. Size was defined as radius (in mm) in the case of radial growth and as tree height (in cm) in the case of length growth, and  $d$  is a parameter which describes the changes in growth rate with tree size. To estimate the maximum likelihood parameter values, we used simulated annealing (Goffe et al. 1994). A series of alternate models were fitted to each dataset. The simplest model (null model) only considered the effect of size on tree growth, and was used to assess the influence of light availability on growth. We also fitted a linear and power model to the data available for each species. The  $R^2$  of the observed vs. predicted regression was used as a measure of goodness of fit of each model, and alternative models were compared using  $\Delta AICc$ , the difference in corrected Akaike Information Criterion (Burnham et al. 2002).

Mortality as a function of radial growth was estimated according to Wyckoff and Clark (2000), who in turn modified the method originally proposed by Kobe et al. (1995). Implementing this method requires the growth rates of live and recently dead saplings together with an estimation of annual mortality rate. Growth rates of living saplings were obtained from the sample collected for growth-light relationships. To obtain the growth rate of dead saplings, 50 recently dead saplings of each species were randomly harvested from the transects, and growth rate was obtained using the method given above for living saplings. The criterion used to consider a sapling as ‘recently dead’ was twig suppleness and the maintenance of some needles. We used a parametric option to allow for comparison among species (Kunstler et al. 2005), where the growth-mortality function for each species can be calculated as:

Equation 2

$$p(d|g) = \frac{\theta}{\left[ \theta + \frac{(1 - \theta)}{Q} \right]}$$

where  $p(d|g)$  is the growth-mortality function,  $\theta$  is the overall mortality rate, and  $Q$  is the ratio of the growth rates ( $g_i$ ) of living ( $g_l$ ) and dead ( $g_d$ ) saplings. These growth rates were estimated by adjusting

the dataset to a gamma density distribution using the maximum likelihood method, with the likelihood of the gamma density being:

Equation 3

$$L(G_d | \lambda_d, \rho_d) = \prod_{i=1}^D \frac{\lambda_d^{\rho_d}}{\Gamma(\rho_d)} g_i^{(\rho_d-1)} \exp(-\lambda_d g_i)$$

where  $G_d$  represents the data set for the growth rates of dead saplings and  $\Gamma$  is the gamma function, while  $\lambda_d$  and  $\rho_d$  are *shape* and *scale*, the fitted parameters for the gamma density. The same approach was used for live saplings, but likelihood took parameters  $\lambda_l$  and  $\rho_l$  and the dataset was  $G_l$ . Overall mortality rate  $\theta$  was estimated, for each species, from 100x5 m transects in which all recently dead and living saplings were counted. Parameters were estimated using simulated annealing, as specified above. Mortality as a function of light availability was obtained by combining equations [1] and [2]. For a given light availability, growth was estimated from equation [1] for an individual with a radius of 20 mm (the dataset average). Then, growth ratio  $Q$  was estimated, and annual probability of mortality was obtained from equation [3]. To assess sapling performance, probability of survival as a function of light availability was calculated for an average-size sapling and for two situations, i.e. *i*) over five years and *ii*) over the number of years needed to become adult (diameter > 75 mm).

## Architecture and crown morphology

For the data set of living saplings, a set of architectural traits was calculated: apical and lateral average growth and slenderness (as the ratio between tree height and diameter). Crown morphology was assessed by crown depth (the ratio between crown height and total tree height), crown slenderness (the ratio between crown height and crown diameter) and apical dominance, estimated by plagiotropy index (the ratio between apical and lateral growth). The influence of light availability and ontogenetic effects on these morphological and architectural traits was determined by analysis of covariance, where species was a factor and %PPFD and tree size were covariates. %PPFD was transformed to its logarithm when necessary to achieve normality of residuals and homoscedasticity. Differences in slope coefficients between species were tested by examining the significance of the



interaction term between species and %PPFD or tree size, respectively. Unless otherwise specified, significance was set at  $P\text{-value} < 0.05$ .

## Results

### Growth and mortality as a function of light availability

The key role of light in both apical and radial growth was strongly supported by our data, the full Michaelis-Menten model presenting in all cases a much lower AICc value than the null model, in which no influence of light was considered (Table 1). Furthermore, the Michaelis-Menten model fitted well for all the datasets ( $R^2$  ranging between 0.53 and 0.8; Table 1). At low light levels, the slope of the function relating apical growth and light was similar for the three species. However, fir rapidly reached its asymptotic growth and thus both pines outgrew fir growth as light availability increased above 15% (Figure 1). At full sun, Scots pine showed higher maximum apical growth rate than mountain pine, the differences between the two species becoming important for light values above 40%. Both pines increased their radial growth almost linearly in response to light availability (Table 1; Figure 1). In contrast, fir reached its maximum growth rate at a light availability of 20%.

In all cases, radial growth over the last three years was consistently higher for living saplings than for dead saplings (Table 2). Silver fir had the lowest probability of mortality for any given growth rate or light level, with almost no variation across the entire data range (Figure 2). Scots pine showed the greatest probability of mortality at low and intermediate growth rates, clearly above that observed for mountain pine, but its mortality rate dropped below mountain pine's for growth rates higher than  $0.9 \text{ mm} \cdot \text{year}^{-1}$  (Figure 2).

Among-species trends in mortality for different light levels were similar to those observed for different growth rates (Figure 3a). Thus, while silver fir consistently showed the highest likelihood of survival (above 0.8) at any given light level, both pines sharply increased their probability of survival as light availability increased. Survival rates for mountain pine and Scots pine reached 50% at 12%

and 20% of full sun, respectively. However, the Scots pine survival likelihood surpassed that of mountain pine at light levels above 40%. At full light, mountain pine and silver fir showed a similar maximum survival rate of 0.9 over a period of five years (Figure 3a), whereas the survival rate of Scots pine sapling with no light limitation reached values up to 99%. Maximum survival probability did also differ among species when considering time needed to reach adulthood (defined as a tree with  $\text{dbh} > 7.5 \text{ cm}$ ), mainly as a consequence of differential growth rates (Figure 3b). At low light levels, fir showed the highest survival rates, but as it took more than 25 years for a fir to become an adult (data not shown), its survival rate never reached more than 60%, whatever the light level. In the case of pines, their high mortality rate at low light conditions almost prevented them reaching adulthood at any given light level below 15%. Above this value, their probabilities of reaching adult size rapidly increased, driven by a lower mortality rate associated with higher radial growths. Both pines showed similar survival trends at light levels below 50%. Differences between Scots pine and mountain pine at low light were lower than observed for a five-year period due to the accumulated effect of lower mortality for Scots pine at any growth rate above  $1 \text{ mm} \cdot \text{year}^{-1}$  (Figure 3b), but differences in full sun were bigger as a consequence of the higher radial growth rate of Scots pine

### **Architectural and morphological plasticity in response to light availability**

The models explained more than a half of total observed variability for all the architectural and morphological variables analyzed (R-squared ranging from 0.59 to 0.81), except for slenderness (R-squared = 0.29; Figure 4). All architectural traits significantly changed with variation in light availability and the response was species-specific (Table 3). In effect, response of apical and lateral growth to changes in light environment was significantly higher for Scots pine than the other two species ( $P < 0.001$ , data not shown), while no significant differences in growth rate variation were observed between mountain pine and silver fir (apical growth:  $P = 0.09$ ; LG:  $P = 0.96$ ; data not shown). Growth curves for Scots pine intersected the x- axis at  $\% \text{PPFD} = 10$ , demonstrating almost no apical or lateral growth below that light level (Figure 4a). In contrast, mountain pine and silver fir

showed positive growth values even at very low light levels, but the apical growth of Scots pine rapidly overgrew both of them (at %PPFD = 9 and 22, respectively). Growth of lateral branches tended to follow the same pattern, but in this case the growth of fir was the highest at low light and Scots pine only became the fastest-growing species at light levels above 25%, while mountain pine could not rival with fir growth even at full sunlight (Figure 4a). Slenderness was significantly reduced with increasing light conditions for all three species (Figure 4c), but the decrease was significantly sharper for Scots pine, which decreased slenderness by more than 50%, than for the other two species, whose response was not statistically different ( $P = 0.270$ ; data not shown). All three architectural variables increased with tree size (Figure 4), but species-specific differences in response were only observed for apical growth (Table 3). Silver fir showed a weak response in apical growth with increasing tree size, whereas both pines showed a significantly higher response ( $P < 0.01$ ), but without significant between-pine differences ( $P = 0.237$ ; data not shown).

Crown morphology also varied among species. Mountain pine and silver fir showed a slight yet significant increase in crown depth as light availability increased, without difference between the two species ( $P = 0.205$ ; data not shown). However, Scots pine gave a significantly higher response slope ( $P < 0.001$ ; data not shown), as its crown depth increased from 0.31 at 10% PPFD to over 0.85 at full-sun (Figure 5a). Both pines showed two-fold higher crown slenderness values than silver fir, but no effect of light availability on crown slenderness was observed (Table 3; Figure 5c). Silver fir presented a significantly lower plagiotropy index than both pines at any light level. Even though differences were bigger at deep shade as fir reduced its apical dominance to less than one (Figure 5e), no species-specific responses to light variations were observed ( $P = 0.089$ ; Table 3). Size also induced variation in crown morphology variables. Mountain pine and fir increased the depth of their crown as saplings got bigger, but with no significant difference in their response ( $P = 0.101$ ; data not shown). However, Scots pine showed the opposite trend (Figure 5b). Crowns also tended to be slenderer as tree size increased, whatever the species considered (Figure 5d). In the case of plagiotropy index, fir values decreased as saplings got bigger, whereas both pines showed the opposite trend (Figure 5e).

## Discussion

Our results correctly matched previously established classifications of shade tolerance proposed by Ellenberg (1992), who assigned a value of three (shade-tolerant, the minimum value for tree species) to silver fir and eight (half-light to full-light species) to Scots pine and mountain pine. Radial growth in deep shade conditions (below 10% of full sun) was almost double for silver fir than for pines, but fir reached its maximum growth at around 20% of incident light, as observed by Robakowski et al. (2003). Hence, both pines rapidly outgrew fir as more light became available. However, although differences between fir and pines were especially important in low light conditions, silver fir showed the lowest annual mortality rate for any given light level. Therefore our results confirm that the higher survival ability of silver fir in low light conditions is due to its ability to maintain a higher radial growth in light-limiting environments, which has traditionally been considered the main general explanation of shade tolerance (Bazzaz 1979, Givnish 1988, Pacala et al. 1993, Wright et al. 1998, Lin et al. 2002), but also to an intrinsic ability to withstand low radial growth rates, as more recently suggested for shade-tolerant species (Pacala et al. 1994, Kobe et al. 1997, Vieilledent et al. 2010). Although differences in tolerance were much slighter between pine species than between genera, Scots pine showed a higher mortality risk in shaded environments than mountain pine, despite no significant differences in relative growth. Therefore, differences in mortality between both pines are due to lack of ability of Scots pine to survive at low radial growth rather than to any enhanced growth ability of mountain pine.

Recently, a series of studies have suggested a relationship between shade tolerance (understood as survival at deep shade) and the ability to suppress height growth when faced with shade conditions (Messier et al. 1999, Williams et al. 1999, Kneeshaw et al. 2006). These studies assert that shade-intolerant species would favor height growth, even in shade conditions. If the enhanced growth results in a greater light availability, for example by rapidly attaining the forest canopy, it will favor sapling performance. Conversely, if it does not result in an advantage in light interception, then the increase in height would cause the saplings to incur higher respiration and maintenance costs that would

subsequently increase mortality rate (Givnish 1988, Messier et al. 1999, Claveau et al. 2002). The patterns of maximum height for live and dead saplings observed in our study agree with this hypothesis, and reveal two opposite behaviors when having to withstand shade conditions. Both pine species show a “shade-escaping” strategy, maintaining an enhanced height growth (much higher than silver fir) even in shade. However, only pines not growing above a determined height – slightly above three meters – are likely to survive (Figure 6). In contrast, silver fir appears to develop a conservative resource-use strategy in which growth is reduced to increase the chances of survival, a typical “shade-tolerant” strategy (Canham 1988, Beaudet et al. 1998, Claveau et al. 2002, Sánchez-Gómez et al. 2006a).

Silver fir showed little variation in its architectural and crown morphological patterns, *i.e.* low plasticity to changes in available light, except for plagiotropy index. The observed weak apical dominance in the shade was caused by fir’s ability to reduce height growth and is a common trait in shade-tolerant firs (Figure 7). Nevertheless, low plasticity in crown depth conflicts with the observed patterns for other *Abies* species which usually vary their crown shape from a conical form in full sun to a flat-topped form in understory shade (Kohyama 1980, O’Connell et al. 1994). If the observed crown depth values at low light matched previous findings reported elsewhere (Figure 7), the scant maximum crown depth revealed a limited ability of *Abies alba* saplings to exploit high-light conditions, as observed by Grassi and Bagnaresi (2001). Conversely, *Pinus sylvestris* showed the highest plasticity in apical growth, lateral growth, slenderness and crown depth, conflicting with patterns of low plasticity commonly observed for pines (Figure 7). High slenderness values were probably a consequence of the “shade-escaping” strategy of Scots pine and its sharp reduction of crown depth in shade may be interpreted as an attempt to increase survival chances by reducing maintenance costs associated with non-photosynthetic tissues (Beaudet and Messier 1998; Givnish 1988). Finally, mountain pine showed an intermediate and moderate behavior matching previous results for *Pinus* species (Figure 7).

The negative correlation between morphological plasticity and survival in deep shade that we observed in this study has already been linked in Mediterranean areas to the high costs of the “shade-escaping” strategy for intolerant species (Sánchez-Gómez et al. 2006a). Simultaneous adaptation of plants to a combined gradient of different ecological factors requires compromises that can restrict the competitive success of the species (Valladares et al. 2002, Sánchez-Gómez et al. 2008). Since both Scots pine and silver fir find their upper limit of distribution in the studied ecotone, deviations from expected patterns may also correspond to species-specific responses to these compromises. In Mediterranean areas, for example, drought-induced stress caused little change in Scots pine response to light, whereas limited morphological and physiological plasticity in *Abies alba* has been related to its low drought resistance (Grassi et al. 2001, Robakowski et al. 2003, Robakowski et al. 2004).

Sapling size also modulated the architectural response of the three species to changing light conditions. Both pines showed a high response in apical growth as saplings got bigger. This could be related to existence putative correlation between apical growth and sapling size, but as saplings of all sizes were sampled in every light ambiance, it could also imply a higher selective pressure against pines with greater growth, whereas moderate or limited growth for firs would be part of a strategy to avoid growing above the maximum sustainable height (Messier et al. 1999, Claveau et al. 2002, Kneeshaw et al. 2006).

## **Ecological implications**

Brokaw and Busing (2000) defined three premises to coexistence through niche partitioning in gaps: (i) the existence of a light availability gradient; (ii) specific differential distribution along that transect and (iii) a species-specific trade-off in performance along the gradient. All the three were accomplished by the ecotones studied here. Furthermore, light availability explained a major part of observed variability in growth and mortality for the three studied species, thus emphasizing the important role of light in the demographic processes in the studied forests. Pines growth patterns were adapted to maximize performance in high light ambiances, yet incurring high mortality in closed

understory. Conversely, fir optimizes performance in shade but cannot compete with pines in light levels above 60%. The generalized densification of mountain forests caused by reduced logging can nevertheless favor the progressive establishment of advanced regeneration of fir in the understory (Robakowski et al. 2004, Aunós et al. 2007). Although fir presented the lowest annual mortality rate for any given light level, its limited radial growth makes it incur higher accumulated mortality risk during its lifespan. Both pines only showed slight differences in growth and mortality, even though the observed differences in plasticity could imply a higher adaptative potential for Scots pine to a changing environment. If the minimum temperatures currently acting as a barrier to upward spread of Scots pine were to rise as expected (IPCC 2007), subsequent enhanced growth would mean a competitive advantage for this species. Furthermore, as mountain pine has had to adapt its morphology and physiology to tough environmental conditions this could constrain its ability of responding to changes in light availability. In short, if silver fir is the species most favored by a lack of management (that creates shaded understories where pine has few opportunities to regenerate), and if temperature no longer limits Scots pine performance (favoring its colonization of open areas), the current land-use and climate change context are expected to culminate in a progressive upward shift of the lower distribution limit of *Pinus uncinata* stands.

## Acknowledgements

This research was primarily supported by the Spanish Ministry of Science and Innovation via the DINAMIX project (AGL2009-13270-C02) and the Consolider-Ingenio Montes project (CSD2008-00040). The Spanish Ministry of Science provided Lluís Coll with support through a Ramon y Cajal contract (RYC-2009-04985), and the Spanish Ministry of Education provided support to Aitor Ameztegui through a predoctoral grant (FPU Program - AP2007-01663). Christian Messier provided helpful comments on the manuscript. We also thank Sara Bastien-Henri and Santiago Martín for valuable help during field sampling and laboratory processing and the ‘Parc Natural de l’Alt Pirineu’ for kindly giving us permission to access the park and sample the data.

## References

- Anderson, R.C., Loucks, O.L. & Swain, A.M. 1969. Herbaceous Response to Canopy Cover, Light Intensity, and Throughfall Precipitation in Coniferous Forests. *Ecology* 50: 255-263.
- Aunós, A., Martínez, E. & Blanco, R. 2007. Tipología selvícola para los abetales españoles de *Abies alba* Mill. *Investigaciones Agrarias: Sistemas y Recursos Forestales* 16: 52-64.
- Baker, F.S. 1949. A Revised Tolerance Table. *J. For.* 47: 179-181.
- Bazzaz, F.A. 1979. Physiological Ecology of Plant Succession. *Annu. Rev. Ecol. Syst.* 10: 351-371.
- Beaudet, M. & Messier, C. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Can. J. For. Res.* 28: 1007-1015.
- Blanco, E., Casado, M.A., Costa, M., Escribano, R., García, M., Génova, M., Gómez, A., Gómez, F., Moreno, J.C., Morla, C., Regato, P. & Sainz, H. 2005. *Los bosques ibéricos: una interpretación geobotánica*. Ed. Planeta, Barcelona.
- Brokaw, N. & Busing, R.T. 2000. Niche versus chance and tree diversity in forest gaps. *Tree* 15: 183-188.
- Burnham, K.P. & Anderson, D. 2002. *Model Selection and Multi-Model Inference*. Springer.
- Camarero, J.J., Gutierrez, E. & Fortin, M.J. 2000. Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. *For. Ecol. Manag.* 134: 1-16.
- Camprodon, J. 2001. Tratamientos forestales y conservación de la fauna vertebrada. In: Camprodon, J. & Plana, E. (eds.) pp. 173-227. Universitat de Barcelona, Barcelona.
- Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70: 548-550.
- Canham, C.D. 1988. Growth and canopy architecture of shade-tolerant trees - Response to canopy gaps. *Ecology* 69: 786-795.
- Canham, C.D., Kobe, R.K., Latty, E.F. & Chazdon, R.L. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. *Oecologia* 121: 1-11.
- Claveau, Y., Messier, C., Comeau, P.G. & Coates, K.D. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. *Can. J. For. Res.* 32: 458-468.
- Chen, H.Y.H. 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. *Can. J. For. Res.* 27: 1383-1393.
- Chen, H.Y.H., Klinka, K. & Kayahara, G.J. 1996. Effects of light on growth, crown architecture, and specific leaf area for naturally established *Pinus contorta* var. *latifolia* and *Pseudotsuga menziesii* var. *glauca* saplings. *Can. J. For. Res.* 26: 1149-1157.



- Delagrange, S., Messier, C., Lechowicz, M.J. & Dizengremel, P. 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiology* 24: 775-784.
- Ellenberg, H. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18.
- Gilmore, D.W. & Seymour, R.S. 1997. Crown architecture of *Abies balsamea* from four canopy positions. *Tree Physiol.* 17: 71-80.
- Givnish, T.J. 1988. Adaptation to Sun and Shade: a Whole-Plant Perspective. *Functional Plant Biology* 15: 63-92.
- Goffe, W.L., Ferrier, G.D. & Rogers, J. 1994. Global optimization of statistical functions with simulated annealing. *Journal of Econometrics* 60: 65-99.
- Gracia, M., Montane, F., Pique, J. & Retana, J. 2007. Overstory structure and topographic gradients determining diversity and abundance of understory shrub species in temperate forests in central Pyrenees (NE Spain). *Forest Ecology and Management* 242: 391-397.
- Grassi, G. & Bagnaresi, U. 2001. Foliar morphological and physiological plasticity in *Picea abies* and *Abies alba* saplings along a natural light gradient. *Tree Physiol.* 21: 959-967.
- Gratzer, G., Darabant, A., Chhetri, P.B., Rai, P.B. & Eckmullner, O. 2004. Interspecific variation in the response of growth, crown morphology, and survivorship to light of six tree species in the conifer belt of the Bhutan Himalayas. *Canadian Journal of Forest Research* 34: 1093-1107.
- Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. 2010. Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. *Oikos* 119: 475-484.
- IPCC 2007. *Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Solomon S et al. Cambridge University Press, UK and New York, NY, USA.
- Kneeshaw, D.D., Kobe, R.K., Coates, K.D. & Messier, C. 2006. Sapling size influences shade tolerance ranking among southern boreal tree species. *Journal of Ecology* 94: 471-480.
- Kobe, R.K. 1996. Intraspecific Variation in Sapling Mortality and Growth Predicts Geographic Variation in Forest Composition. *Ecological Monographs* 66: 181-181.
- Kobe, R.K. & Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Canadian Journal of Forest Research* 27: 227-236.
- Kobe, R.K., Pacala, S.W., Silander, J.A. & Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* 5: 517-532.
- Kohyama, T. 1980. Growth pattern of *Abies mariesii* saplings under conditions of open-growth and suppression. *The Botanical Magazine Tokyo* 93: 13-24.
- Kunstler, G., Curt, T., Bouchaud, M. & Lepart, J. 2005. Growth, mortality, and morphological response of European beech and downy oak along a light gradient in sub-Mediterranean forest. *Canadian Journal of Forest Research* 35: 1657-1668.
- Lin, J., Harcombe, P.A., Fulton, M.R. & Hall, R.W. 2002. Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. *Oecologia* 132: 428-435.

- Lusk, C.H., Falster, D.S., Jara-Vergara, C.K., Jimenez-Castillo, M. & Saldaña-Mendoza, A. 2008. Ontogenetic variation in light requirements of juvenile rainforest evergreens. *Functional Ecology* 22: 454-459.
- Lussier, J.-M., Gagné, R. & Bélanger, G. 2004. Improving visual detection of growth rings of diffuse-porous hardwoods using fluorescence. *Forestry Chronicle* 80: 612-616.
- Mason, W.L. & Alía, R. 2000. Current and future status of Scots pine (*Pinus sylvestris* L.) forests in Europe. *Investigaciones Agrarias: Sistemas y Recursos Forestales* Fuera de serie: 317-335.
- Messier, C., Doucet, R., Ruel, J.C., Claveau, Y., Kelly, C. & Lechowicz, M.J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Canadian Journal of Forest Research* 29: 812-823.
- Messier, C. & Puttonen, P. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands: the basis for a quick and efficient method of characterizing light. *Canadian Journal of Forest Research* 25: 343-354.
- Neilson, R.P. 1993. TRANSIENT ECOTONE RESPONSE TO CLIMATIC CHANGE : SOME CONCEPTUAL AND MODELLING APPROACHES. *Ecological Applications* 3: 385-395.
- Niinemets, Ü. 2006. The controversy over traits conferring shade-tolerance in trees: ontogenetic changes revisited. *Journal of Ecology* 94: 464-470.
- O'Connell, B.M. & Kelty, M.J. 1994. Crown architecture of understory and open-grown white pine (*Pinus strobus* L.) saplings. *Tree Physiol.* 14: 89-102.
- Pacala, S.W., Canham, C.D. & Silander, J.A. 1993. Forest models defined by field-measurements. 1. The design of a northeastern forest simulator. *Canadian Journal of Forest Research* 23: 1980-1988.
- Pacala, S.W., Canham, C.D., Silander, J.A. & Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* 24: 2172-2183.
- Parent, S. & Messier, C. 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. *Canadian Journal of Forest Research* 26: 151-154.
- Peñuelas, J. & Boada, M. 2003. A global change-induced biome shift in the Montseny mountains ( NE Spain ). *Global Change Biology* 9: 131-140.
- Peñuelas, J., Ogaya, R., Boada, M. & Jump, A.S. 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography* 30: 829-837.
- Resco, V., Fischer, C. & Colinas, C. 2006. Climate Change Effects on Mediterranean Forests and Preventive Measures. *New For.* 33: 29-40.
- Robakowski, P., Montpied, P. & Dreyer, E. 2003. Plasticity of morphological and physiological traits in response to different levels of irradiance in seedlings of silver fir ( *Abies alba* Mill). *Trees - Structure and Function* 17: 431-441.

- Robakowski, P., Wyka, T., Samardakiewicz, S. & Kierzkowski, D. 2004. Growth, photosynthesis, and needle structure of silver fir ( Mill.) seedlings under different canopies. *For. Ecol. Manag.* 201: 211-227.
- Ruiz de la Torre, J. 2006. *Flora Mayor*. Dirección General para la Biodiversidad. Ministerio de Medio Ambiente, Madrid.
- Sánchez-Gómez, D., Valladares, F. & Zavala, M.A. 2006a. Functional traits and plasticity in response to light in seedlings of four Iberian forest tree species. *Tree physiology* 26: 1425-1433.
- Sánchez-Gómez, D., Valladares, F. & Zavala, M.A. 2006b. Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. *New Phytologist* 170: 795-806.
- Sánchez-Gómez, D., Zavala, M.A., B., D., Urbieto, I.R. & Valladares, F. 2008. Rank reversals in tree growth along tree size , competition and climatic gradients for four forest canopy dominant species in Central Spain. *Annals of Forest Science* 65: 605-605.
- Takahashi, K. 1996. Plastic Response of Crown Architecture to Crowding in Understorey Trees of Two Co-dominating Conifers. *Ann. Bot.* 77: 159-164.
- Tucker, G., Hinckley, T., Leverenz, J. & Jiang, S. 1987. Adjustments of foliar morphology in the acclimation of understory Pacific silver fir following clearcutting. *Forest Ecology and Management* 21: 249-268.
- Valladares, F., Manuel, J., Aranda, I., Balaguer, L. & Dizengremel, P. 2002. The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. *Trees* 16: 395-403.
- Valladares, F. & Niinemets, Ü. 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annual Review of Ecology Evolution and Systematics* 39: 237-257.
- Valladares, F., Sánchez-Gómez, D. & Zavala, M.A. 2006. Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology* 94: 1103-1116.
- Vetaas, O.R. 2002. Realized and potential climate niches: a comparison of four *Rhododendron* tree species. *Journal of Biogeography* 29: 545-554.
- Vieilledent, G., Courbaud, B., Kunstler, G. & Dhôte, J.-F. 2010. Mortality of silver fir and Norway Spruce in the Western Alps – a semi-parametric approach combining size-dependent and growth-dependent mortality. *Ann. For. Sci.* 67: 305-316.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.
- Whitmore, T.C. 1989. Canopy Gaps and the Two Major Groups of Forest Trees. *Ecology* 70: 536-538.
- Williams, H., Messier, C. & Kneeshaw, D.D. 1999. Effects of light availability and sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine. *Canadian Journal of Forest Research* 29: 222-231.

**Post-print version.** The final version of this article can be found at:

Ameztegui A, Coll L (2011) Tree dynamics and coexistence in the montane-subalpine ecotone: the role of different light-induced strategies. *Journal of Vegetation Science* 22 (6): 1049-1061.

DOI: [10.1111/j.1654-1103.2011.01316.x](https://doi.org/10.1111/j.1654-1103.2011.01316.x)

Woodward, F.I. & Williams, B.G. 1987. Climate and plant distribution at global and local scales. *Vegetatio* 69: 189-197.

Wright, E.F., Coates, K.D., Canham, C.D. & Bartemucci, P. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. *Canadian Journal of Forest Research* 28: 871-886.

Wyckoff, P.H. & Clark, J.S. 2000. Predicting tree mortality from diameter growth: a comparison of maximum likelihood and Bayesian approaches. *Canadian Journal of Forest Research* 30: 156-167.

Wyckoff, P.H. & Clark, J.S. 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *Journal of Ecology* 90: 604-615.

Table 1. Parameter estimates for Michaelis-Menten growth-light function for (a) apical growth; (b) radial growth.

Apical growth						
Species	N	a	s	d	R <sup>2</sup>	ΔAICc
<i>A. alba</i>	94	0.445 [0.396; 0.498]	0.029 [0.024; 0.035]	0.656 [0.642; 0.668]	0.691	79.17
<i>P. sylvestris</i>	98	6.428 [5.564; 7.486]	0.043 [0.040; 0.046]	0.488 [0.483; 0.493]	0.842	136.89
<i>P. uncinata</i>	96	0.809 [0.669; 0.977]	0.013 [0.011; 0.015]	0.756 [0.741; 0.767]	0.535	35.54
Radial growth						
Species	N	a	s	D	R <sup>2</sup>	ΔAICc
<i>A. alba</i>	94	17.43 [15.63; 19.41]	2.16 [1.73; 2.70]	0.449 [0.421; 0.473]	0.591	66.10
<i>P. sylvestris</i>	98	4031.8 [40.30; 10000.0]	0.0071 [0.0068; 0.0076]	0.436 [0.418; 0.449]	0.802	148.49
<i>P. uncinata</i>	96	3069.8 [0.23; 10000.0]	0.0015 [0.0013; 0.0016]	0.93 [0.90; 0.96]	0.579	88.53

Note: Parameter estimates for radial growth of *Abies alba* cannot be directly compared with the rest of species as the dependent variable was multiplied by 100 to avoid anormal residual behavior. N is sample size and *a*, *s* and *d* are the fitted parameters of the Michaelis-Menten functions. R<sup>2</sup> is the regression coefficient of the observed vs. predicted equation and ΔAICc is the decrease in AICc for the selected Michaelis-Menten model as compared with a null model in which no light effect on growth is considered. Values in brackets are the 2-unit support intervals for the parameter estimates.

**Post-print version.** The final version of this article can be found at:

Ameztegui A, Coll L (2011) Tree dynamics and coexistence in the montane-subalpine ecotone: the role of different light-induced strategies. *Journal of Vegetation Science* 22 (6): 1049-1061.

DOI: [10.1111/j.1654-1103.2011.01316.x](https://doi.org/10.1111/j.1654-1103.2011.01316.x)

Table 2. Estimated parameters of shape ( $\rho$ ) and scale ( $\lambda$ ) for the adjusted gamma distribution of radial growth for live and dead saplings

Species	Live			Dead			Annual Mortality Rate
	Growth rate (mm·year <sup>-1</sup> )	$\lambda$	$\rho$	Growth rate (mm·year <sup>-1</sup> )	$\lambda$	$\rho$	
<i>A. alba</i>	0.30	0.11 [0.09; 0.14]	2.62 [2.17; 3.07]	0.17	0.10 [0.08-0.13]	2.50 [1.89; 3.10]	0.033
<i>P. sylvestris</i>	1.26	1.06 [0.86; 1.26]	1.892 [1.56; 2.22]	0.33	0.60 [0.41-0.79]	1.13 [0.80; 1.46]	0.066
<i>P. uncinata</i>	0.77	0.45 [0.38; 0.53e]	1.71 [1.40; 2.03]	0.25	0.39 [0.27-0.50]	1.22 [0.89; 1.55]	0.110

Values in brackets are the 2-unit support intervals for the parameter estimates.

**Post-print version.** The final version of this article can be found at:

Ameztegui A, Coll L (2011) Tree dynamics and coexistence in the montane-subalpine ecotone: the role of different light-induced strategies. *Journal of Vegetation Science* 22 (6): 1049-1061.

DOI: [10.1111/j.1654-1103.2011.01316.x](https://doi.org/10.1111/j.1654-1103.2011.01316.x)

Table 3. Summary of ANCOVA P values (values in bold indicate significance at  $\alpha = 5\%$ ) for the relationship between plant architecture, crown morphology and tree size (TH), light (L) and species (SP) and interactions.

<b>Variable</b>	<b>SP</b>	<b>L</b>	<b>TH</b>	<b>SPxL</b>	<b>SPxTH</b>
<i>Architecture</i>					
Apical growth	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.002</b>
Lateral growth	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.188
Slenderness	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.172
<i>Crown Morphology</i>					
Plagiortropy index	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.089	<b>0.018</b>
Crown Depth	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.201	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Crown Slenderness	<b>0.001</b>	0.132	<b>&lt;0.001</b>	0.263	<b>0.002</b>

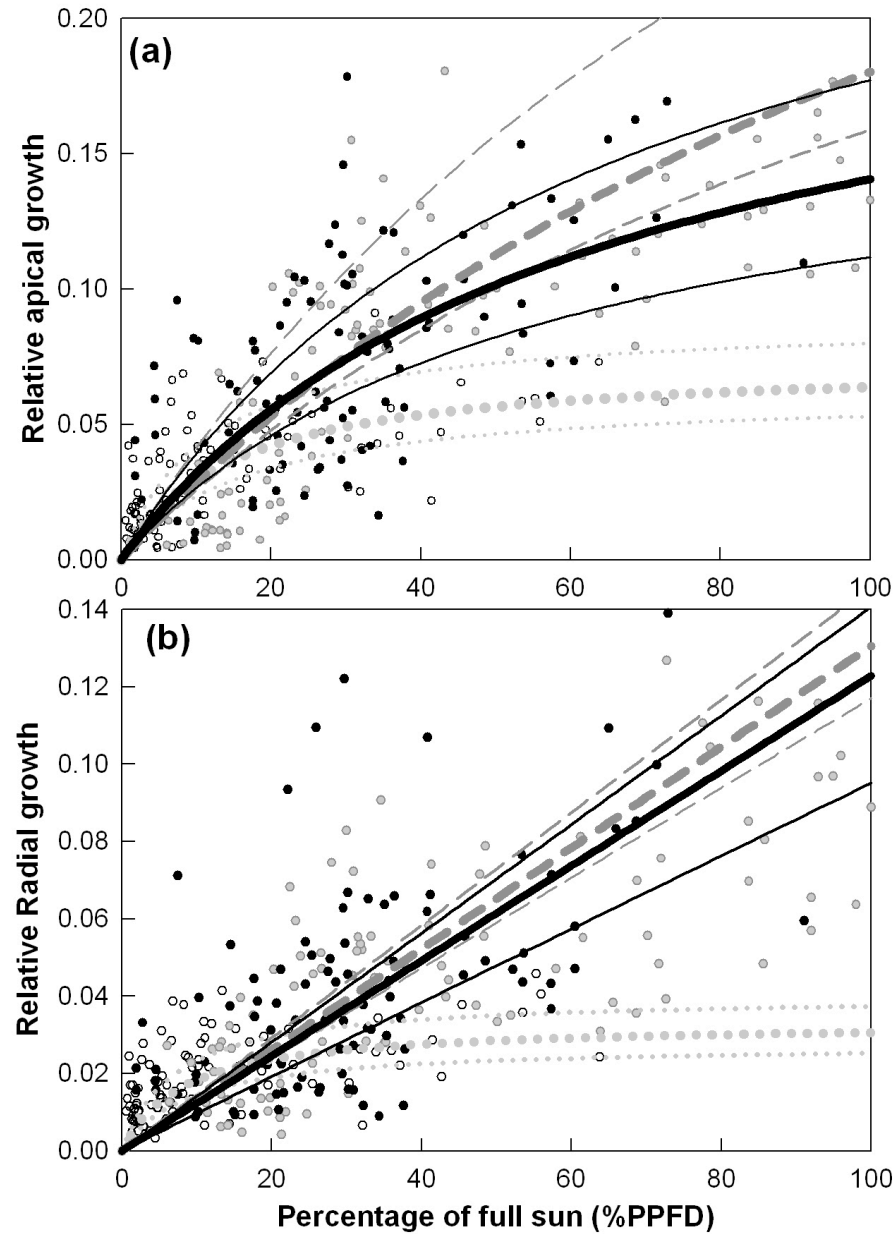


Figure 1. Response of (a) relative apical growth and (b) relative radial growth to increases in light availability. Dots represent observed values for 94 *Abies alba* (unfilled dots), 98 *Pinus sylvestris* (grey dots) and 96 *Pinus uncinata* (black dots) saplings. Thick lines correspond to the adjusted Michaelis-Menten function for a sapling with average radius (20 mm) and height (180 cm), with the parameters shown in Table 1 for *Pinus uncinata* (black), *Pinus sylvestris* (dark-grey) and *Abies alba* (light-grey). Dashed lines represent upper and lower growth predictions constructed with minimum and maximum values of the 2-unit support intervals for parameter estimates.



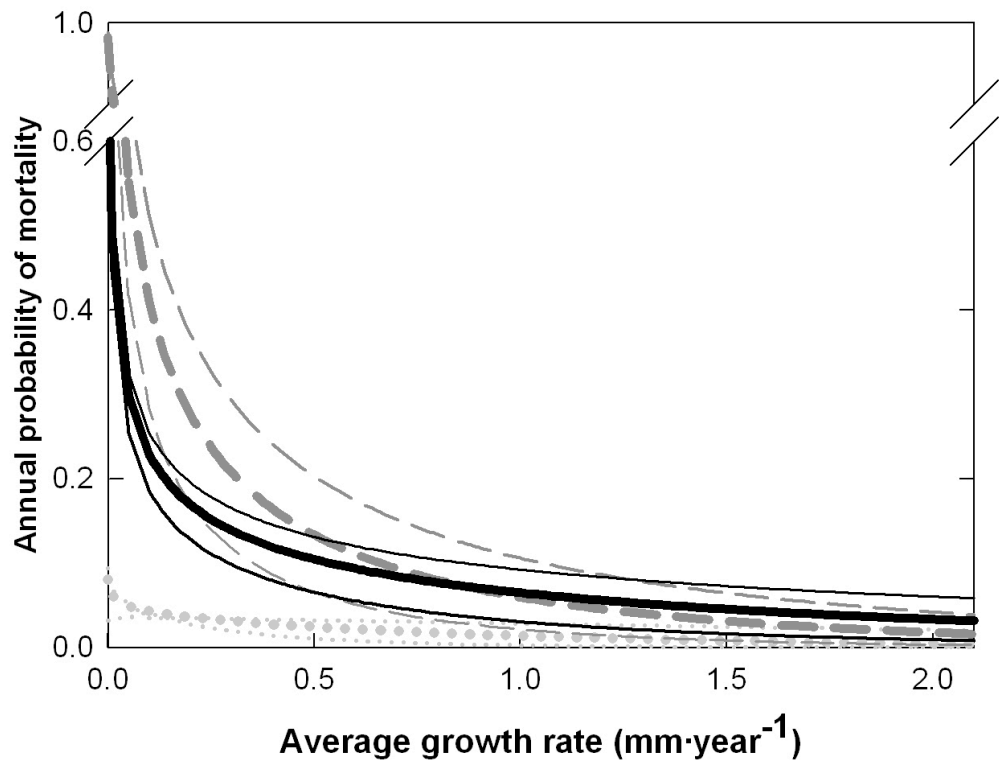


Figure 2. Annual probability of mortality for a sapling as a function of average radial growth rate. Growth rate was calculated for a sapling with average radius (20 mm). Thick lines represent modeled annual probability of mortality, while dashed lines represent upper and lower growth predictions constructed with minimum and maximum values of the 2-unit support intervals for parameter estimates: *Pinus uncinata* (black), *Pinus sylvestris* (dark-grey) and *Abies alba* (light-grey).

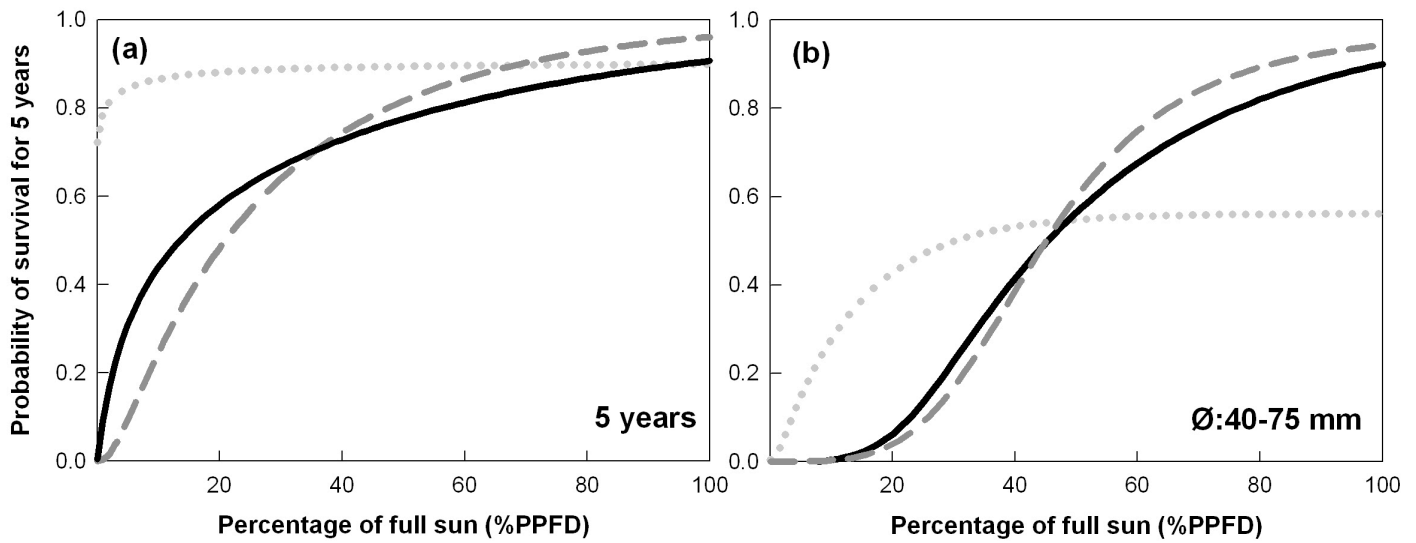


Figure 3. Probability of survival for an average sapling over (a) a five-year period; and (b) the time needed to reach a diameter of 75 mm (the average sapling had a diameter of 40 mm). Species are: *Pinus uncinata* (black lines), *Pinus sylvestris* (dark-grey lines) and *Abies alba* (light-grey lines).

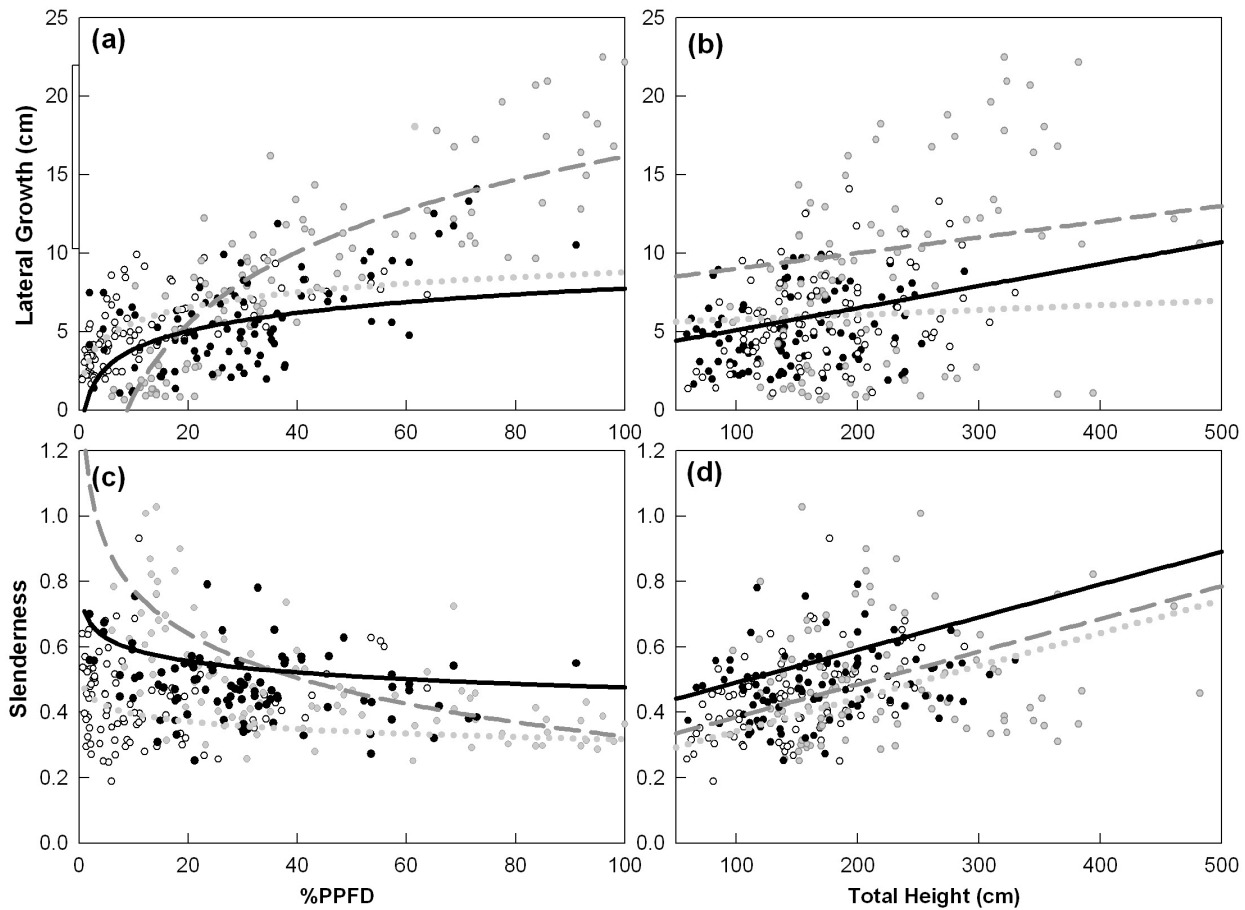


Figure 4. Effect of light availability and sapling size on sapling architecture. Dots represent observed values, while lines correspond to ANCOVA models. Explanatory variable not indicated in the x axis is set to the average for each species. Species are: *Pinus uncinata* (black solid dots and black lines), *Pinus sylvestris* (grey dots and dashed lines) and *Abies alba* (unfilled dots and dotted lines).

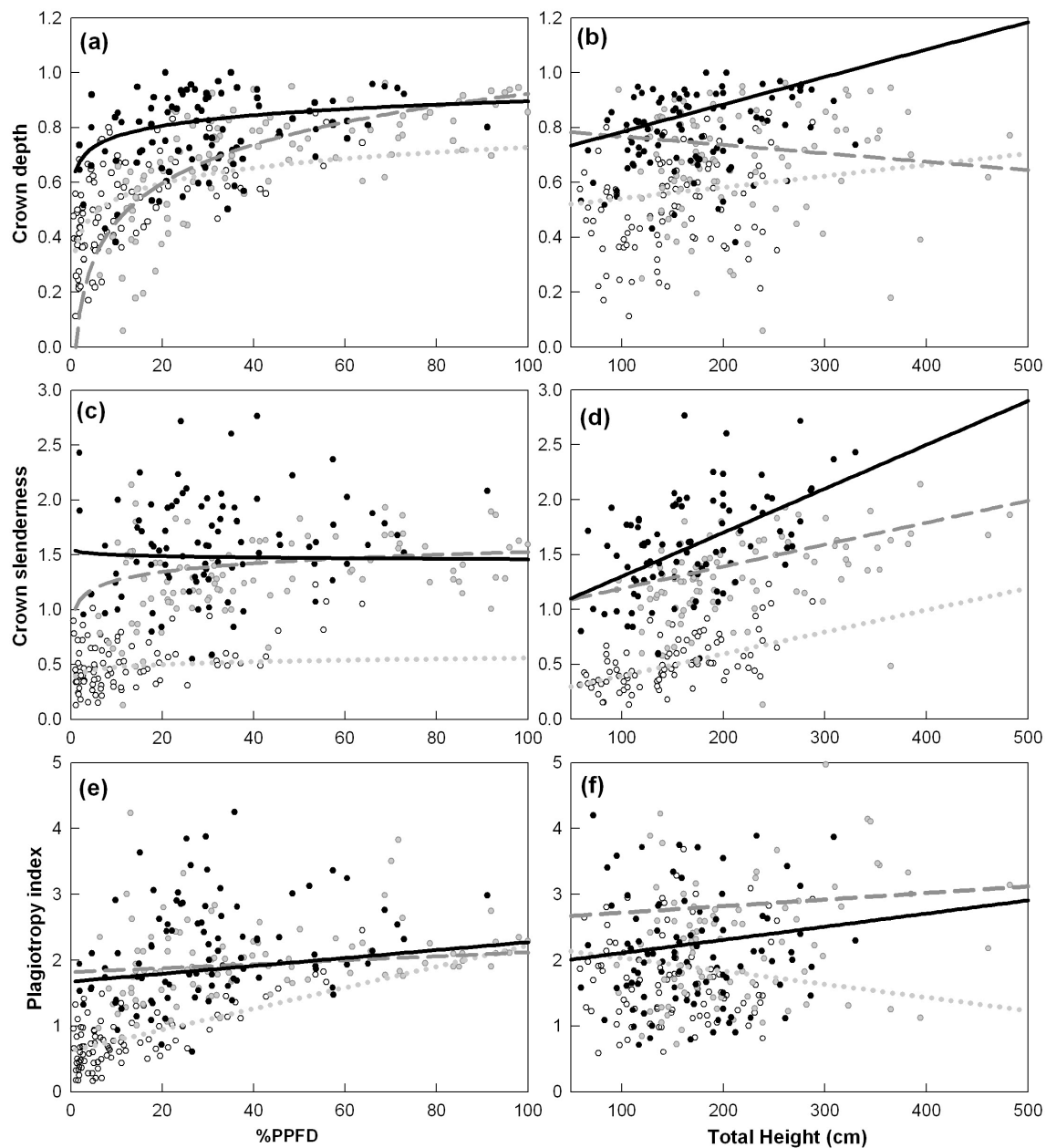


Figure 5. Effect of light availability and sapling size on crown morphology traits. Dots represent observed values, while lines correspond to ANCOVA models. Explanatory variable not indicated in the x axis is set to the average for each species. Species are: *Pinus uncinata* (black solid dots and black lines), *Pinus sylvestris* (grey dots and dashed lines) and *Abies alba* (unfilled dots and dotted lines).

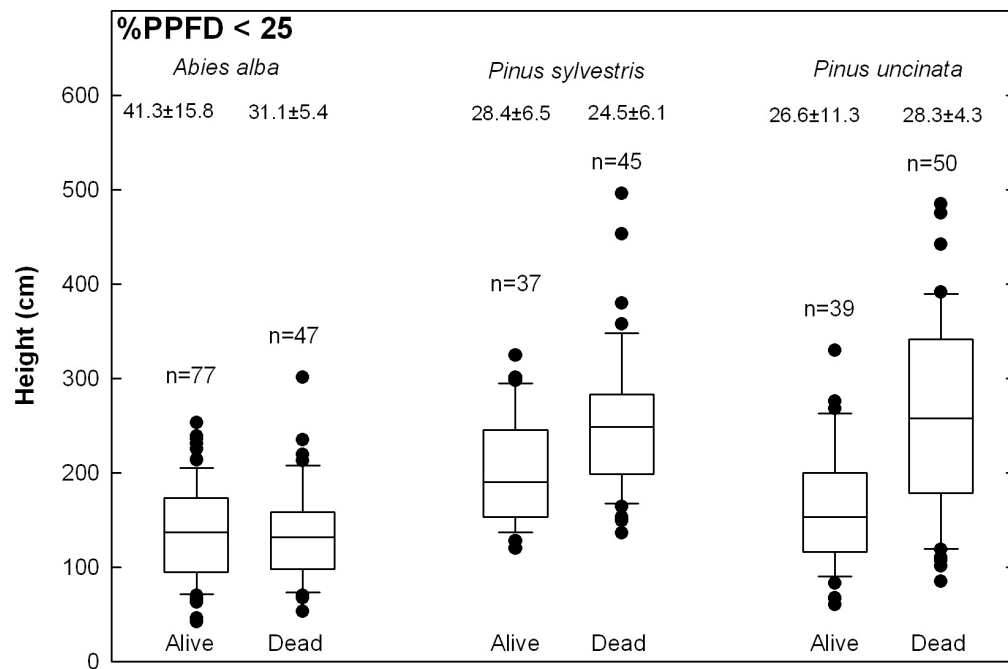


Figure 6. Box-plots for total height of living and dead saplings of the three studied species in shade-conditions (below 25% of PPFD). N represents the sample size, while numbers below species name are the mean±standard deviation of saplings age in years.

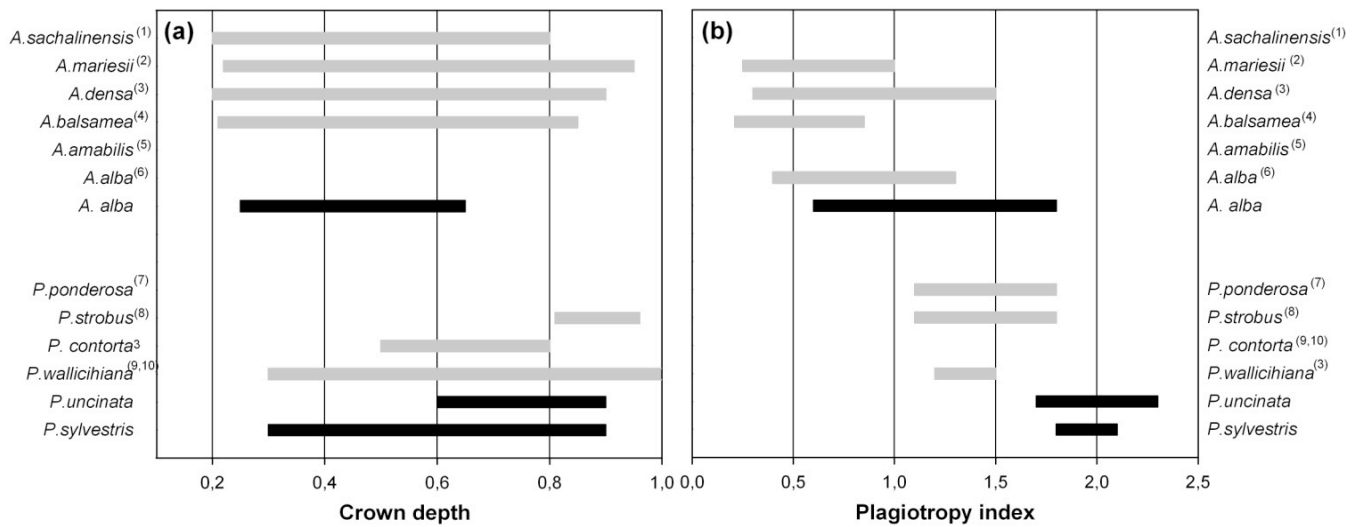


Figure 7. Minimum (at deep shade) and maximum (in full sunlight) values of (a) crown depth and (b) plagiotropy index for several *Abies* and *Pinus* species. Black bars represented observed values in this study. Grey bars represent values obtained from literature review: (1) Takahashi (1996); (2) Kohyama (1980); (3) Gratzner et al. (2004); (4) Gilmore and Seymour (1997); (5) Tucker et al. (1987); (6) Robakowski et al. (2004); (7) Chen (1997); (8) O'Connell and Kelty (1994); (9) Chen et al. (1996); (10) Williams et al. (1999)